ECOLOGY OF FISHES IN THE AMAZON AND CONGO BASINS

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Abstract. Some relationships between the great diversity of fishes and physical and biological aspects of the environment in the Amazon and Congo basins are discussed. Aspects of physical environment considered are rainfall regimes; stabilizing influence of forests; seasonal fluctuations in water level; white water, clear water, and black water; relative accessibility of Amazon and Congo basins to marine fishes; tidal conditions in the lower Amazon; shoreline and islands; river anastomoses and connections with adjacent basins; stream captures; unique or peculiar biotypes; causes of massive mortality of fishes. The main adaptive significance of parental care in Amazon and Congo fishes is evidently related to reproduction in deoxygenated waters. The following topics are considered under biological interactions: fishes with brilliant coloration or conspicuous markings; association of similarly colored species of fishes in mixed schools; fishes of minute size; responses to predation; and partitioning of food resources. About one third of the paper is devoted to discussion of trophic adaptations and feeding habits. The topics considered are predatory fishes; scale-eating characoids; fin-eating characoids; feeding habits of "parasitic" trichomycterid catfishes; parallelism in feeding habits of "weakly electrogenic" fishes in the Amazon and Congo basins; plankton-feeding fishes; deposit feeders; and feeding habits of characins and other fishes in Amazonian rainforest streams.

INTRODUCTION

An overwhelming proportion of the species of fishes in continental fresh waters are primary freshwater forms. This means that they are unable to live in salt water, and have had a long history separate from that of marine fishes. The great majority of these freshwater fishes are members of a single group, the Ostariophysi. In contrast to tropical marine shore fishes, which have had only one principal center of radiation—the Indo-Pacific—ostariophysans in Africa, South America, and Eurasia have radiated largely in isolation from one another. Asia and Africa, of course, share many ostariophysan elements. There is some indication that the South American and older African ostariophysan elements had a common origin. The formation of the Amazon basin provided the opportunity for a remarkable radiation of Ostariophysi. The Amazon and Congo basins have more kinds of fishes than any other river basins in the world, and both exhibit a high degree of endemism.

One of the principal reasons tropical fish faunas are richer than temperate ones is that they have not been as adversely affected by glaciation. Pleistocene glaciation probably caused extinction or withdrawal of marine shore fishes in the higher latitudes, especially in the North Atlantic (Briggs, 1970). It is unlikely that fishes live more than a few miles inward under the ice caps. Freshwater fishes in most of North America and northern Eurasia were wiped out by Pleistocene glaciation. Western Europe now has a depauperate fish fauna of only about 60 species, all or almost all derived from stocks that populated the area in postglacial times.

It may be well to express here my suspicion that the richness of the Congo and Amazon fish faunas is not necessarily ancient. Fishes have undergone considerable diversification, with great increase in the number of species, in lakes less than five million years old. I do not believe that lakes represent the only ecological situation in which explosive adaptive radiations of fishes have occurred. It is conceivable that the present Amazonian fish fauna, with its large number of species, is the product of only a few million years of evolution from an original stock of two or three hundred founder species. Some of the founders, of course, would represent groups of considerable antiquity.

Draining two and a quarter million square miles, the Amazon basin is the largest river basin in the world. Its mouth discharges an average of three to four million cubic feet of water per second. The Congo, discharging 1.4×10^6 cubic feet per second from slightly over one and a half million square miles, is the second largest. The vast area of these basins, with abundant water and varied habitats, undoubtedly contributes to the large number of fish species in them. Habitats such as streams with high gradients or streams draining dry ground (igarapés de terra firma) are sometimes separated by hundreds of miles. Meandering creates a regular succession of habitats in the main courses of the big rivers. The high percentage of the basins at base level, along with the relatively stable existence of so much aquatic habitat, favors the existence of very large numbers of individuals, which in turn is conducive to the existence of large numbers of species (Preston, 1962).

As of 1967 (the last year for which the Zoological Record has been issued) approximately 1300 species of fishes had been recorded from the Amazon and 560 from the Congo (including the Lualaba River but not lakes Bangweolu and Moeru). The Mississippi basin, in comparison, with an area (1,244,000 square miles) almost as large as that of the Congo basin, has only 250 species. It is unlikely that many species remain unrecorded in the relatively well-studied Mississippi, but the numbers known from the Amazon and Congo will undoubtedly increase considerably as systematic studies continue.

The limnology, seasonal changes and some biological aspects of the rivers, lagos, flooded forest (igapó) and streams (igarapés) that constitute the main habitats of Amazon fishes are described by Sioli (1964, 1967) and Fittkau (1964, 1967). The ecology of fish habitats in the cuvette centrale of the Congo basin, similar in many respects to that in the Amazon, is described by Gosse (1963) and Matthes (1964). McConnell (1964) described the ecological groupings of fishes and effects of the seasonal cycle on the fishes in the Rupununi savanna of British Guiana. Many of her remarks are applicable to the Amazon basin, especially to the savanna parts of it. Most, if not all, of the species in the Rupununi are present in the Amazon. McConnell (1969) reviewed some factors contributing to speciation in tropical freshwater fishes, and many of her remarks apply indirectly or directly to fishes in the Amazon and Congo basins. Knöppel (1970) reported in detail on the stomach contents of a large number of fish species from small rain forest streams near Manaus. Myers (1947, 1949a) gave a general account of Amazonian fishes and their ecology.

The main part of this paper is divided into two sections. The first section deals with the interactions of fishes and physical aspects of environment in the Amazon and Congo basins, the second section with biological interactions among fishes in the Amazon and Congo basins. The rest of this introduction provides a brief sketch of the main groups of ostariophysans and other fishes under consideration. Readers familiar with these groups may turn directly to the main part of the paper if they wish. In drafts of this paper I tended to include extraneous notes about species occurrence, etc., which might distract readers interested mainly in the discussion of ecology and adaptations. These notes, indicated by arabic numerals in the text, are given at the end of the paper. They are of concern primarily to systematists and zoogeographers.

Ostariophysi—the Predominant Fishes in Both Basins

In the Amazon 43 percent of the fishes are characoids, 39 percent siluroids, and 3 percent gymnotoids. In the Congo 15 percent are characoids, 23 percent siluroids, and 16 percent cyprinoids. All of these fishes belong to the order Ostariophysi, which thus comprises 85 percent of the Amazon's and 54 percent of the Congo's fish fauna. Ostariophysi differ from all other fishes in the manner in which some of the neural arches and ribs of the first four vertebrae are modified into an apparatus, the Weberian apparatus, which conducts vibrations from the swim bladder to the inner ear. There is no precise understanding of how the Weberian apparatus affects sound (and pressure?) perception, nor is much known about the effects of sound on the behavior of ostariophysans in nature. It is generally agreed, however, that they are "acoustic specialists," and that their worldwide predominance in fresh waters is somehow linked with the Weberian apparatus. Experimental work with various ostariophysans indicates that their auditory sensitivity and range is greater than in many other fishes. Of considerable interest is whether they have directional hearing, i. e., can localize the source of a sound by means of their auditory apparatus. Most fishes apparently have nondirectional hearing, but directional hearing evidently occurs in several groups (see Moulton and Dixon, 1967: 195). The only freshwater fishes thought to have directional hearing are Ostariophysi and perhaps mormyroids. Kleerekoper and Chagnon (1954) and Delco (1960) reported directional hearing in three species of North American minnows. Whatever the nature of its role in perception, it seems highly likely the Weberian apparatus has increased the opportunities for interactions between fish species.

Characoids. Characoids or characins are mostly laterally-compressed, open-water fishes, active in the daytime, many of them silvery or iridescent. They usually have jaw teeth, often of a highly complex nature (Roberts, 1967), and invariably lack barbels. With few exceptions, they are not known to produce biologically significant sounds (almost all fishes produce noises incidental to feeding and locomotion). Of the large groups of fishes inhabiting the earth's fresh waters, characoids (as a group) exhibit the least tolerance for salt or brackish water. They occur only in Africa and Central and South America. Their presence in Central America undoubtedly is the result of recent invasion, and it is unreasonable to believe that they could have reached Africa and South America by way of Europe and North America without leaving the least trace of their passage (Myers, 1966). The only fossils identified with certainty as characins are African, or South or Central American (Weitzman, 1960). In the light of evidence for Continental Drift and for characoid antiquity (Greenwood et al., 1966; Roberts, 1969) it is reasonable to think that characins were present in South America before it separated fully from Africa.

Gymnotoids. Gymnotoids, the so-called electric eels, all have specialized electrogenic and electrosensory organs. The quality of the electric discharges is characteristic of each species. The gymnotoid that has received the most scientific attention, the famous electric eel (*Electrophorus electricus* Linnaeus) studied by Alexander von Humboldt, Faraday, and others, has a very powerful discharge. The discharges of other gymnotoids are too weak for us to sense without the help of instruments and have only recently come to our attention. We are just beginning to appreciate the roles played by gymnotoid electric organs in object location and in intra- and interspecific behavior. Many of the species have specialized trophic structures, and at least some are highly active at night, hiding or even burying in sand during the day. Their mode of swimming is peculiar (Lissmann, 1958; Greenwood et al., 1966: 383–384). The geographical restriction of gymnotoids to part of South and Central America indicates that the group had a later origin. Their greatest diversity (18 genera and 35 species) is in the Amazon basin. They are almost as well represented as this in the Guianas and the Orinoco basin. Outside these areas their diversity declines markedly. A few species, belonging to wide-ranging genera, occur north as far as southern Central America (a single species reaching Guatemala) and south to the Plata basin. They are almost absent west of the Andes (a single wide-ranging species reaching coastal Ecuador), and are absent in the numerous Atlantic coast drainages between the mouths of the Rio São Francisco and the Rio Paraíba. Gymnotoids were derived from characoids.

Siluroids. Siluroids or catfishes typically are denser-than-water, bottom-dwelling fishes with flattened bellies and nocturnal habits. The dentition usually consists of numerous simple conical elements in bands of varying thickness. The barbels, usually two or three pairs, sometimes (as in Bagridae) four pairs, are almost invariably present (one exception in South America, none in Africa) and serve as tactile and gustatory organs. In the African Mochokidae (represented by 37 species in the Congo) the barbels are highly branched. In contrast to characins, catfishes are noisy. They produce sound from various anatomical structures; the most familiar catfish sounds are due to stridulation between pectoral spine and girdle. Of the 31 families of catfishes recognized by Greenwood et al. (1966), eight occur in Africa (three of them endemic) and 14 in South and Central America (all but Ariidae endemic). Catfishes are more widely distributed geographically than any other ostariophysans, and their inter- and intrafamilial relationships are not well understood. Two of the living families (Ariidae and Plotosidae) are predominantly marine. Representatives of a South American endemic family, the Aspredinidae, occur along the Guiana coast (Myers, 1960a). Several people are working on the morphology and classification of catfishes on a worldwide basis, and much new information relevant to their zoogeographic history will be available soon. The startling diversity of endemic catfishes in South America and the presence in southern South America of the only two species in the family Diplomystidae, the most primitive of living catfishes, indicate that catfishes, like characoids, were in South America long ago, certainly in the Mesozoic.

Cyprinoids. Minnows, the only group of cyprinoids in the Congo basin, more or less resemble characins except they have protrusible jaws and frequently one or two pairs of small barbels, while jaw teeth and adipose fin invariably are absent (most characins and catfishes have a rayless adipose fin behind the dorsal fin). The lower pharyngeal teeth, however, are highly modified and despite their lack of jaw teeth minnows exhibit considerable diversification in feeding structures, as shown by Matthes (1963) for African forms. The cyprinoids are perhaps more diverse in North America and certainly much more diverse in Asia than they are in Africa. It is generally thought that they originated in Asia. However this may be, the number of minnow species in Africa is very high, especially in Ethiopia, Southern Africa, and in the rockier headwaters of many of the bigger tropical rivers, including the Congo.

Non-ostariophysan Primary and Secondary Freshwater Fishes

South America is not rich in the number of major groups of freshwater fishes it harbors. The only primary freshwater fishes in South America other than Ostariophysi are a genus of Lepidosirenidae, two genera of Osteoglossidae, and two genera of Nandidae. The secondary freshwater fishes (*sensu* Myers, 1949b) consist of Cichlidae, Cyprinodontidae, Poeciliidae, Galaxiidae, and Percichthyidae. All of these families of primary and secondary fishes excepting Galaxiidae and Percichthyidae are present in the Amazon basin, and all of them excepting Poeciliidae and Percichthyidae also occur in Africa.

The primary and secondary freshwater fish fauna of Africa is much more complex. It can be broken down into three main categories: 1) groups shared with South America—ostariophysans excluding Cyprinidae, Lepidosirenidae, Osteoglossidae, Nandidae, Cichlidae, Cyprinodontidae, and Galaxiidae; 2) groups shared with Asia, and which probably originated in Asia—perhaps complicated by the fact that they may have been centered in India when India was closer to Africa than to Asia—Notopteridae, Cyprinidae, Mastacembelidae, Anabantidae, and Ophiocephalidae or Channidae; and 3) an unparalleled assemblage of archaic primary freshwater forms known only from Africa—Polypteridae, Denticipitidae, Pantodontidae, Phractolaemidae, Kneriidae, Mormyridae, and Gymnarchidae. Practically all of the families reach their greatest diversity in Africa in the Congo basin, excepting Nandidae, Denticipitidae, and Gymnarchidae, which are unknown from there. The weakly electrogenic mormyroid fishes parallel gymnotoids in many ways (see pp. 140–141).

INTERRELATIONS BETWEEN FISHES AND THE PHYSICAL ENVIRONMENT IN THE CONGO AND AMAZON BASINS

Since the Amazon and Congo basins straddle the equator, they have two rainfall regimes. Most of the Amazon basin lies south of the equator, and in this portion the rainy season is generally from December through April or May. During the rest of the year the rain decreases somewhat. In virtually the entire Rio Branco basin, the Rio Negro basin north of Uaupés, and most of Colombian Amazon, on the other hand, the rainy season is generally from March to November or December, or from May through August, and the dry season (at least in the savanna area of the Rio Branco) is somewhat more pronounced. In the Congo basin the great Ubanghi River from north of the equator and the smaller but numerous southern tributaries are in high water at opposite times of the year; thus the maximum and minimum average rates of flow of 75,000 and 50,000 cubic meters per second at Kinshasa are close. The water level in the Amazon River is mainly determined by contributions from southern tributaries and run-off from melting snow in the Andes. Snow melts during much of the year, and rainy seasons are prolonged (it may rain a lot during the so-called dry season). The bulk of these contributions comes at somewhat different times of the year. The relative difference between maximum and minimum water levels in the lower courses of the Amazon and Congo rivers, although considerable, is less than in any other river in the world. The absence of a period of severe desiccation has no doubt enhanced the evolution of rich faunal diversity.

Forests and relative environmental stability. Today forests cover a large part of the Congo and Amazon basins but this has not always been so. During much of the Recent and Pleistocene periods the forests retreated and advanced in response to cyclical climatic changes. Their present range lies somewhere between the greatest and least extents of the past. In the Amazon basin much of Brazil's Roraima Territory is "campo" or savanna. Great tongues of campo extend between the southern tributaries of the Middle and Lower Amazon. Montane forests and gallery forests along the great tributaries and the main Congo and Amazon rivers were the portions of forest that would have suffered least from long dry periods. Certainly some montane forests persisted, and perhaps the main gallery forests never disappeared. The forests undoubtedly mitigated the adverse effects of dry periods on the fish fauna. On a shorter time scale, they contribute greatly to over-all wetness and temperature stability in the basins. Forest soils and swamps retain a vast quantity of water, which is relinquished throughout the year. Transpiration keeps the air laden with moisture and lengthens the rainy season.

Seasonal fluctuations in water level. Seasonal fluctuations in water level have profound effects on feeding, reproduction and dispersal of fishes (Matthes, 1964; McConnell, 1964). During high water more food is available, and many fishes move into the flooded lands to feed and to reproduce. Growth is rapid and fishes are widely dispersed. As the waters go down, food becomes scarcer for most fishes except predators. Losses to predation are greatest during low water, when fishes are least dispersed. The effects, however, are not nearly so great as in savanna rivers such as the Zambesi, in which the flow during the marked dry season is a small fraction of that during flood time, and massive fish mortalities are an annual event except in unusually wet years. The seasonal fluctuations mean that certain habitats exist only part of the time, and this must play a very important role in fish distribution. It should also be noted that these cyclic changes are more predictable than some other kinds of variability (especially in the temperate zones), and allow adaptive responses to evolve, thus increasing the effective environmental heterogeneity—and increasing rather than decreasing the species diversity.

The forest streams may be flooded in the wet season or go down so much in the dry season that the fishes must either leave or accommodate to great changes. Such constantly changing conditions alter drastically the local faunal composition. During any intensive collecting in the Amazon or Congo, a good proportion of species obtained in a given locale are likely to be either recently arrived or in the process of moving away from habitats that became unfavorable. Thus a rotenone collection in an igarapé may yield 70 or 80 species, but only a third or less will be represented by fair numbers of specimens. Even when such a collection comprises one or two thousand specimens from a stretch of igarapé one mile long, it frequently happens that a dozen or more species are represented by a single specimen. The indications are that most of these came from populations established elsewhere, that their presence is largely due to chance, and that they will soon disappear unless additional individuals enter the igarapé. However, the species composition of adjacent igarapés that superficially look alike may differ markedly. Occasionally an igarapé has numbers of a species that is absent or represented by a single specimen in collections from other igarapés nearby. Investigation of the physical and biotic components might provide an explanation in some instances, but I suspect that, in addition to subtle differences in environment, chance plays a major role. The fact that many species are represented by widely separated populations over the entire basins probably contributes to evolution and maintenance of species diversity. Certainly it is difficult to conceive of the rapid extinction resulting from biotic factors of species dispersed in so broad a manner. Furthermore, the pattern suggests a favorable model for allopatric speciation.

Physical and biological nature of white water, clear water, and black water rivers. The big rivers of the Amazon basin are of three main types: white water, clear water, and black water. These types are not absolute. Some rivers are intermediate between white and clear, others between clear and black; some rivers may be clear water in the dry season and white water in the rainy season. However, the main Amazon river (known as the Solimões above Manaus) is white water year round, and its largest tributary, the Rio Negro, is black water year round. White water (its color actually tan or café-au-lait) is due to suspended earth; the white water rivers arise in the Andes and are constantly eroding the alluvium from their steep banks. Proceeding up the Solimões from Manaus one is impressed by evidence of landslides (terras caídas) from the steeper banks, some of which must release tens of thousands of tons of earth into the river. The resulting white waters are relatively rich in salts compared with other Amazonian waters (Gibbs, 1970). Because of the silt, they are opaque, and light does not penetrate more than two or three feet, usually much less. Thus they do not support photosynthesizing plant life. The *p*H of the white waters ranges from 6.2 to 7.2 (in part from Sioli, 1967: 31–34).

Seen from a distance or from the air, the black water rivers appear quite black. In a glass the water is the color of weak tea and is quite clear. The black water rivers of Amazonas apparently originate in lowland areas with bleached, sandy podsol soils (Klinge, 1967). These soils, and perhaps decaying organic matter in the flooded forests, provide humic coloring substances which give the water its characteristic tint. Light is effectively cut off about three to six feet below the surface. The mineral content is precipitation dominated (Gibbs, 1970) and so low that the water may be considered "distilled water slightly polluted with organic compounds." Virtually no primary productivity occurs in black water rivers. Furthermore, the black waters are highly acid, with *p*H ranging from 3.8 to 4.9 (Sioli, 1967: 34).

The characteristics of the basins and the water chemistry play profound roles in determining the distribution and abundance of animals in the Amazon basin. In the evenings an incredible variety of moths and dipterous insects, including numerous species of mosquitoes, are commonly attracted to boats plying a white water river. In the daytime one is liable to be bitten by hordes of Simuliidae. On the other hand, during 25 days and nights spent on the Rio Negro (above Manaus) at widely different times of the year, I failed to encounter a single biting insect (to my immense relief!) and noted that even moths were relatively scarce. It may be that the extremely acid conditions of the black waters in the Rio Negro are lethal for most aquatic insects. Perhaps largely because of the absence of insects, terrestrial animals such as frogs and lizards (relatively abundant along the Solimões) were seldom encountered in my ramblings along the shore. Fish populations are probably lower here than elsewhere, although there is no data to support this. In the black water and white water rivers most of the food available for fishes must come from terrestrial sources (Marlier, 1967) or floating vegetation. There is probably very little food for nonpredaceous fishes in the main Rio Negro, which presumably find most of their food in habitats peripheral to the main stream, especially during periods of high water. In the white water rivers earth slides probably bring considerable amounts of plants and lower animal life that serve as food directly into the main channels, and production along the main watercourse by floating vegetation probably is also greater. Men who have learned to fish in the Rio Negro are sometimes conceded to be the best fishermen in Amazonas. Some black water rivers are known as "rios de fome" because there is little food to support the population. Extremely little human habitation is found along the main Rio Negro between Manaus and the mouth of the Rio Branco. The only towns are small and usually located near the mouths of clear or white water affluents. Along the Solimões River habitations occur every quarter- or half-mile over long stretches. The "moradores" usually have flower and vegetable gardens and small feijão plantations. The Solimões has large towns and cities, but these are usually some distance up black water rivers or just downstream from a large black water outlet, which provides a degree of protection from insects.

The clear water rivers are more diverse in origin and possess a broader range of *p*H values—from 4.5 to 7.8—than black and white water rivers, indicating that they are chemically (and biologically) a heterogeneous assemblage. The only character they share is the relative lack of organic coloring materials and suspended matter (Sioli, 1967: 33–34).

In the Congo basin the rivers can be similarly classified according to their waters. The southern tributaries are mostly black water, and during part of the year the main Congo River is a deep-tinted brown, approaching black water. The Ubanghi River is white, however, when it passes its flood waters to the Congo River. At this time contributions from the southern black water tributaries are at their lowest. The Ubanghi is the only true white water tributary in the Congo basin; the rest are either black water or clear water. The main Congo River never becomes sufficiently laden with silt to be considered a white water river. In the Congo River, as in the Amazon, food chains must originate largely on the land. The relatively recent introduction and widespread establishment of *Eichhornia* in the Congo basin must have greatly increased the relative contribution of floating plants to food available in the main river courses. There are many varieties of floating plants in the Amazon basin, including *Eichhornia*, but these are little in evidence along the main river channels. Along much of the Congo River *Eichhornia* is extremely abundant. Its roots offer haven and presumably food to many small species of fishes and to the young of many larger species of catfishes, characins, and mormyroids in Stanley Pool (personal observation).

Relative accessibility of Amazon and Congo basins to marine fishes. Most of the African continent is relatively high above sea level, and marine fishes ascending rivers usually do not get very far inland (Marlier, 1967). Most fishes in the cuvette centrale of the Congo are primary freshwater fishes (*sensu* Myers, 1949b). Two families, Cyprinodontidae and Cichlidae, are secondary freshwater fishes that have undergone extensive radiations in fresh water. The remaining secondary freshwater fishes in the cuvette centrale belong to four families—Clupeidae, Eleotridae, Centropomidae, and Tetraodontidae—which are better represented in salt water than in fresh water. The particular groups involved, however, entered the fresh waters of Africa a very long time ago, and must have invaded the Congo basin via other river systems instead of directly from the sea. The clupeids are members of the Pellonulinae, also present in fresh water in tropical Asia.[1] All but two or three of the eleven or twelve species of Pellonulinae in the Congo basin appear to be endemic. The Eleotridae are represented by a single small species, *Kribia nana*. This species, or one closely related to it, is found in many rivers in West Africa. The genus is known only from fresh water. The Centropomidae are represented by *Lates niloticus*, present in most of the bigger rivers of tropical Africa. Finally, the Tetraodontidae (with two species of *Tetraodon* in African rivers outside the Congo basin) are represented in the Congo by four species, three of them endemic. Not a single sporadic marine invader has been reliably recorded from the Congo River above the lower rapids.[2]

In contrast to the Congo, the Amazon basin is relatively open to invaders from the sea. Fourteen families of fishes that are predominantly marine have species widely distributed in the Amazon basin. The elasmobranch families Carcharhinidae and Pristidae, each with a single species in the Amazon, are probably sporadic invaders.[3] Clupeidae (herrings) are represented by five species, at least two endemic; Engraulidae (anchovies) by a dozen species, about half endemic; Belonidae (needlefishes) by three species, two endemic; Hemiramphidae (half-beaks) by a single species, *Hyporamphus brederi* (Fernandez-Yepez) (Collette, personal communication); Mugilidae (mullets) by a single species of *Mugil;* Synbranchidae by *Synbranchus marmoratus* (widespread in streams and swamps throughout most of tropical Central and South America); Sciaenidae (croakers or drums) by about ten species, several endemic; Eleotridae by two tiny species of the genus *Microphilypnus* Myers (1927), both endemic; Achiridae (flatfishes) by about nine species, most endemic; Tetraodontidae (puffers) by a single species, *Colomesus psittacus;* and, Batrachoididae (toad-fishes) by an endemic species, *Thalassophryne amazonica* (Collette, 1966a). Thus slightly more than 50 species of fishes belonging to predominantly marine families are widespread in the Amazon basin. About half of them are endemic species. In most instances the ancestral populations probably invaded the Amazon basin directly from the sea. In addition to these 50, many more marine species have been recorded from the lowermost Amazon, especially from Pará. As noted by Marlier (1967) the great extension of brackish waters in the mouth of the Amazon and along the coast has undoubtedly facilitated invasion of the Amazon basin by marine forms. In like manner such conditions must have favored the marine invasion by catfishes of the subfamily Aspredininae, which belong to a family (Aspredinidae) otherwise found only in fresh water. The three genera and four species of Aspredininae are restricted to the lowland, muddy coast of Guiana and Amazonia, occurring in the sea, in brackish waters, and in the estuaries and tidal portions of rivers, including the Amazon delta (Myers, 1960a).

Tidal conditions in the lower Amazon and effect on fish life. Many marine and estuarine fishes ascend the lower courses of tropical rivers with the rising tide. Fishes apt to do this in the lower Amazon delta area include species of Centropomidae, Mugilidae, Belonidae, Sciaenidae, Pomadasyidae, Lutjanidae, Ariidae, Atherinidae, Carangidae, Clupeidae, Engraulidae, and Dasyatidae. Tidal bores (pororóca) occur in much of the delta area (Branner, 1884), and the highest tides are said to exert their influence as far upriver as Santarem. The periodic rise in water level (occurring with great rapidity and force in certain areas) inundates vast areas, submerging terrestrial plants and insects upon which fishes then feed. This regular addition of terrestrial food plus the higher titre of nutrients resulting from mixing with sea water, probably make the mouth and delta the most productive area in the Amazon basin. The variation in the seasonal availability of food is probably least marked here. Schwassmann (1967: 214) reported that schools of *Anableps* near Pará moved close to shore with every rising tide and thought this was correlated with increased feeding on shore insects floated off by the rising water.

Shoreline and islands. The importance of shoreline and islands in the ecology of fishes in the Middle Congo River is stressed by Gosse (1963: 124–138). The islands so characteristic of the Middle Congo River vastly augment the amount of shoreline. It is interesting to note the important role in the development of these islands played by a succession of plant types, from the aquatic grasses such as *Echinochloa* and *Vossia* (les prairies flottantes) which stabilize shifting sand banks to the mature forest on the oldest islands which are not inundated by normal floods. The amount of food available from terrestrial sources, of course, is proportional to the amount of shoreline. In addition, stabler bottom, resulting from slower currents along shore, and clearer water permit greater development of planktonic and benthic plants and animals. Higher plants fringing the shores provide shelter from currents and predators as well as food for the adults and young of many species. Calm and deep places downstream from sand banks and islands and backwaters in which mud and organic detritus accumulate provide particularly suitable habitats for bottom-feeding fishes such as *Labeo, Citharinus*, and *Tilapia*. During the period of high water many of the islands are partially flooded, thus adding to the inundated areas accessible to fishes for feeding and reproduction. In a given section of the Middle Congo River fish productivity probably bears a strong relationship to the number and size of the islands present in it.

The contributions of islands and shoreline outlined above for the Middle Congo also apply to the Amazon. In the evening many small fish (especially characins) move close to the shoreline in order to feed and larger fish including predators and catfishes probably come inshore from deeper waters. In the daytime Curimatidae and Hemiodontidae are to be found feeding over sandy bottom near shore. Beginning about 40 miles above its confluence with the Solimões and continuing some 350 miles upstream, the Rio Negro exhibits a multitude of islands that no other river in the world can rival. For this entire distance there are very few stretches without islands, and such stretches are never more than five miles long. Often there are two or three big islands abreast of each other, and a straight line across the Rio Negro where it attains its greatest widths (15–18 miles) may intersect a dozen islands. High shoreline coefficient, however, cannot make up for the unproductivity of the waters of the Rio Negro, the shores of which must be among the least productive in Amazonas.

River anastomoses and stream captures. "River anastomoses" or interconnections occur in the interior of the Congo basin as well as in the Amazon. Thus the Congo River above Coquilhatville has a series of connections (Chenal de Bosesela, Chenal de Nyoi, etc.) with the Giri River (a large tributary of the Ubanghi), and some of these have connections between themselves. What is probably the greatest complex of river anastomoses in the world occurs between the Solimões and the Rio Japurá in the vicinity of Fonte Boa (Furo Boia, Furo Auati-Paraná), portions of which were explored by the EPA expedition in 1968 (see Acknowledgements). The Auati-Paraná, a navigable furo connecting the Japurá and Solimões and having numerous connections with smaller tributaries, is 125 miles long. Such anastomoses perhaps play a role similar to that of islands in making the flooded forest more accessible to fishes. They must also facilitate dispersal of fishes. It seems likely (although the maps I have do not show any) that connections between the Rio Negro and Solimões exist some 500 miles above their confluence. Such features frequently do not show up on maps, largely because they occur in relatively uninhabited and economically unimportant areas. Even with aerial surveys the smaller connections must be difficult to trace with certainty, and since in any case they would not be navigable, there has been little reason to map them. And of course maps cannot take into account all the minor changes in stream courses and the extent of flooding, which varies so much from year to year. During exceptionally wet years the interconnections available for fish dispersal must be greatly augmented. Since interconnections such as the Auati-Paraná have little or no sources of their own, the direction of flow in them presumably depends on the water level in the rivers they connect. Thus if the Solimões is higher than the Japurá, the Auati-Paraná must flow towards the Japurá, and vice versa; if the water level is similar in both rivers, it has little or no current. If the level of both rivers should drop below that of the Auati-Paraná, it might be drained until only disconnected pools are left.

The Amazon basin has important connections with other basins. The largest of these, the Canal de Casiquiare, links the Rio Negro and Rio Orinoco in Venezuela's Amazonas Province. In Colombia the Amazon basin reputedly is linked to the Magdalena by the Japurá, to the Guaviare (which flows into the Orinoco) by the Uaupés, and to the Inírida (also flowing into the Orinoco) by the Guaniá (an affluent of the Rio Negro). The Mapuera links the Rio Trombetas and Essequibo. In Mato Grosso the Amazon basin supposedly is linked to the Paraguai by the Tapajós and the Guaporé. The Tocantins is linked to the São Francisco. The Casiquiare is a good-sized waterway throughout the year. Some of the other connections probably are broken during particularly dry years. Haseman (1912) was unable to find any connections between the Amazon basin and the Rio Paraguai. It seems likely, however, that within the recent past most of these connections permitted faunal exchanges. The Casiquiare undoubtedly has provided an easy route for exchange of fishes between the Orinoco and Amazon; many species have been recorded from it.[4]

The Orinoco basin and Guiana undoubtedly have been areas of diversification of the fish species independent of the Amazon (as evidenced by large numbers of endemic gymnotoids and doradid catfishes in the Orinoco and such peculiar forms as *Lithoxus* in the Guianas). Exchange between these basins and the Amazon basin has undoubtedly enriched the fish faunas of all three. Despite existing Amazonian connections, however, the fish faunas of the São Francisco and Magdalena retain marked peculiarities (a surprisingly large number of endemic genera of pimelodontids and species of characins in the São Francisco; an extensive radiation of *Astyanax*-like forms in the Magdalena).

There also are some connections between the Congo basin and river systems adjacent to it. Poll (1957) indicated "occasional hydrographic confluences between the Ogowé and Congo" (without stating where they are) as an explanation for the presence in the Ogowé of a number of fish elements characteristic of the Congo. Connections have been reported with the Nile in the region of Garamba; with the Chad basin by affluents of the Ubanghi, Gribingui and Ouham; and with the Zambesi by affluents of the Lualaba (Bell-Cross, 1965). As Gosse (1963: 152) noted, some of these hydrographic connections occur in swampy areas, thus facilitating exchange of certain fishes only.

The Congo and Amazon basins evidently have been growing by stream capture at the expense of adjacent basins. A very important capture was that of the Lualaba, which probably connected earlier with the Upper Nile. The capture apparently occurred at a place named "les portes de l'Enfer" (Poll, 1957: 60). Map study indicates that southern tributaries of the Congo River captured numerous headwaters of westward flowing rivers in Angola. There is a theory that the Tocantins was a separate basin before it was captured by the Amazon. To my knowledge there are no reports of important Amazon or Congo tributaries being captured by adjacent basins. If this is true, it represents a mechanism by which the Amazon and Congo could have gained species from adjacent basins with little or no release of species into them.

Special biotopes. The Congo and Amazon basins provide instances of endemic fishes that are restricted to the special biotopes in which they evidently originated. Several peculiar genera and species (most of them catfishes and cichlids) known only from the lower rapids of the Congo (Poll, 1959, 1966; Roberts, 1968) are almost certainly endemic there and unlikely to be found away from the rapids biotope. Two lakes in the central bowl of the Congo appear to have endemic fishes: lac Tumba has an apparently endemic genus of Characidae (*Clupeopetersius*), an endemic species of catfish (*Eutropius tumbanus*), and an endemic subspecies of cichlid (*Tylochromis lateralis microdon*), and lac Fwa has two endemic genera of Cichlidae (*Cyclopharynx* and *Neopharynx*) and an endemic species of the cichlid genus *Haplochromis* (*H. rheophilus*) (Poll, 1957: 60). The peculiar characoid *Paraphago*, known only from lac Leopold II at Kutu, is probably a relict, rather than an endemic form and may yet be found elsewhere.[5]

As noted by Marlier (1967), all of the present Amazonian lakes are shallow, very young, and markedly dependent on the water level in the rivers with which they are linked; the fishes in them move in and out from the rivers. Although geologically old lakes are absent in the Congo and Amazon basins, the temporary shallow lakes have undoubtedly been a hydrographic feature for a fairly long time. It may be well to consider the possibility that many fishes of the Congo and Amazon are essentially lacustrine forms that must frequently resort to the rivers to find suitable habitats. (This is not to deny the existence of many strictly riverine forms that seldom, if ever, enter lakes, such as cynodontids, various catfishes and gymnotoids, etc.) There is evidence that during wetter times in the Pleistocene much of the interiors of the Amazon basin (Marlier, 1967) and of the Congo basin were covered by a large lake or a series of lakes. One would expect that such conditions had important consequences for the evolution of fishes.

The Amazon does not have any rapids of magnitude comparable to those in the Congo. Nevertheless, four strange genera of trichomycterid catfishes are known only from the São Gabriel rapids on the Rio Negro (Myers, 1944). It seems likely that exploration of other rapids such as those of the Araguaia will divulge peculiar endemic forms. Amazonian headwaters in the Andes provide a great amount of high-gradient stream habitats. The principal fishes found in the highlands streams are astroblepids, loricariids (especially *Ancistrus* and related forms), various trichomycterids and small pimelodontids, and various Tetragonopterinae of small to moderate size. The paucity of this fauna and other evidence suggests it is relatively recent (personal communication from G. R. Smith). The only highly distinctive group that appears to have originated in the Andes is the Astroblepidae. In this family a single genus has speciated extensively. The Himalayas, on the other hand, are the center of distribution for a rich assemblage of highly modified hill stream and mountain torrent fishes (predominantly cyprinoids and siluroids). It is unclear why the Andes have such a relatively poor fish fauna.

Although there are no important mountain ranges in the Congo basin, it is highly probable that several of the species of *Barbus* described by Poll (1967a) from the elevated headwaters of tributary streams in Angola are localized endemics. In most of the big river systems of Africa the greatest representation of endemic *Barbus* species is to be found in rocky headwaters in relative isolation from the richer lowlands fauna.

Extreme physical environmental factors and their effects on fish life. McConnell (1969) hypothesized that biotic pressures are of far greater importance than climatic or physical factors in the evolution of tropical freshwater fishes. There are, however, major physical environmental factors which have met with highly varied evolutionary responses. Concerning highly acid waters (black waters with a *p*H figure sometimes much lower than 5 are a major environmental feature of the Amazon and Congo basins), we have virtually no precise evidence of how the fishes have responded. The blood of most temperate-water fishes is unable to exchange O_2 and CO_2 at *p*H's as low as those in which many tropical freshwater fishes live. Some Amazonian fishes apparently occur only in white or clear waters, perhaps because they are unable to adapt physiologically to the acid conditions encountered in black waters. Certainly many Amazonian fishes are characteristic of black waters, and some of them seem able to reproduce only in water so acid that it would kill many kinds of fishes.

Attention should be called to the "friagens" or cold spells, which cause fish mortalities in the Brazilian territory of Acre and in other parts of Upper Amazonas. Bates (1892: 289) observed mortality of fry of different species of characins at Tefé that he ascribed to a very sudden and quite considerable drop in temperature caused by southerly winds. (Reference cited by J. G. Myers, 1935: 20). According to Geisler (1969), fish mortalities accompanying a friagem may be due not to a drop in temperature, but to the uprising of water with little or no oxygen.

The nonbiotic factors that have had the most obvious, or at least best understood, effects on the evolution of tropical freshwater fishes are deoxygenation and drought. A variety of physiological, morphological, and behavioral adaptations of South American and African freshwater fishes permit them to survive such conditions. Many of these adaptations are well known (see Carter and Beadle, 1931; McConnell, 1964: 132–134) but some probably remain undiscovered. Lewis (1970) documented the morphological and behavioral adaptations that permit cyprinodontids in habitats otherwise totally deficient in O_2 to utilize the O_2-charged water of the first few millimeters immediately below the surface.

Several circumstances lead to waters deficient in O_2 in the Amazon and Congo basins. Black waters, with relatively low *p*H and reducing properties, are particularly subject to deoxygenation. Stagnation occurs in receding flood waters when masses of newly drowned vegetation rot; in lagos that become overgrown with floating vegetation; in the lower courses of some tributaries (such as the Purus and Tapajós) when they are dammed at the confluence by rising water in the main river; and in pools (including those in rapids) during low water. In exceptionally dry years when many igarapés and lagos dry up completely and even big rivers may be reduced to a series of largely disconnected pools, the stagnation must be incredible. At such times massive mortality of fishes is apt to occur. Gadow (1909: 447) reported a prolonged drought on the island of Marajó, in the mouth of the Amazon, that caused swamps and lakes to dry up to the extent that the alligators in them migrated towards the rivers, and many thousands died in the attempt. Spruce (1908, vol. 1: 118) reported that the waters of the Tapajós are sometimes dammed by the Amazon and are rendered stagnant for several weeks, during which time the water is considered very unwholesome. (References cited by J. G. Myers, 1935: 19.) In the Amazon and Orinoco basin stagnation of the waters seems to be associated with some kind of non-specific epizootic which kills fishes and other vertebrates (J. G. Myers, 1935).

In 1839 a drought occurred in the Rio Negro which brought on forest fires, and immense quantities of fishes killed by the heat and drought lay on the sandbanks (Schomburgk, 1931: 181–182). In 1926 during an exceptionally severe dry season in the Rio Negro-Rio Branco area a great fire blazed for over a month destroying vegetation along the lower Rio Negro, and it is said that fishes succumbed (Carvalho, 1952). Fire probably has had little long-term effect on the rain forest.

The occurrence of fires in the rain forest is an example of "less predictable" variability, and the fishes probably show little adaptation to them. In savanna regions, however, where fires are more regularly occurring, fishes may have evolved adaptations to them. The burrowing or estivating habits of lepidosirenids, *Synbranchus*, and other forms may well enhance the probability of their survival in regions frequently subjected to fires.

The role of fire in the ecology of South America undoubtedly has increased since the arrival of man (see Sternberg, 1969:

418–422), and it may be that fires of such magnitude as those of 1839 and 1926 would not have occurred along the Rio Negro unless set by man. In the Rio Uraricoeira area near the Ilha Maracá, I accompanied a fazendeiro who was setting the grasslands of his fazenda ablaze toward the end of the dry season (in April 1969) in order that the tough grass on which his cattle could not feed would be replaced by tender green shoots when the rain came.

Beebe (1945) reported an astonishing variety of fishes from a small "all but dried up mud-hole" in northeastern Venezuela. Some 34 species, comprising six catfishes (a trichomycterid, three callichthyids and two loricariids), fifteen characins, a gymnotid (*Hypopomus*), four cyprinodontoids, six cichlids, *Polycentrus schomburgkii*, and *Synbranchus marmoratus*, were taken from malodorous mud and decayed vegetation covered by damp slime (but no free water) in what was left of a drying pool that had been "almost unswimmable" slime for weeks. He estimated that in another week or ten days without water all would have perished. Of the 15 characins, two are air-breathers. *Copeina* and some of the others perhaps utilize oxygenated water immediately below the surface in a manner similar to that of cyprinodonts. *Copeina* is characteristic of swampy places and stagnant backwaters. But it is difficult to imagine how *Astyanax, Creagrutus, Moenkhausia, Paragoniates, Pristella* and *Serrasalmus* could have survived in such a habitat for as long as they did. Most of the species found in this Venezuelan mud-hole occur in the Amazon basin.

Significance of parental care in Amazon and Congo fishes. McConnell (1969) stated that many tropical freshwater fishes have some form of parental care and implied that biotic factors such as predator pressure are of far greater importance than climatic factors in the evolution of such behavior. This seems to apply to cichlid fishes in lakes Victoria, Tanganyika and Nyasa but not to the riverine fishes of tropical Africa and South America. Whereas an overwhelming proportion of the rich endemic cichlid fauna of these three lakes practice oral brooding, such behavior is far less common in riverine Cichlidae in Africa, and in South America, where it has been reported only in some species of *Geophagus.* The explanation for this remarkable behavioral dichotomy probably lies in relatively simple considerations. In the still, clear littoral waters of the lakes the eggs and young are less readily dispersed and far more susceptible to visually oriented predators. Under riverine conditions the eggs are likely to be separated from the parents by current; moreover, in the black waters and white waters of many tropical rivers, the eggs and young would be extremely difficult to detect visually by predators, and perhaps even more important, by the parents themselves.

In tropical riverine fishes of Africa, South America, and Asia, parental care occurs mainly in fishes in which adults spend at least part of the time in swamps or other oxygen-deficient habitats; many are capable of air-breathing. These fishes, if they reproduce in such habitats, are usually obliged to care for the young. In African and South American lungfishes a nest is constructed that is subsequently guarded and aerated by the male. Notopteridae, osteoglossoids, and Pantodontidae are air-breathers and guard the young. *Gymnarchus,* which is probably capable of air-breathing, makes a floating nest of plants in dense swamps; it is the only mormyroid known to guard the young. Young *Gymnarchus* have external gills with numerous fine filaments and a highly vascularized, enlarged yolk sac, both structures playing an important role in gas exchanges. No other mormyroids have such structures. Parental care might be expected of *Polypterus;* none has been recorded. In Asia the largest group of freshwater fishes with parental care is the air-breathing anabantoids. These fishes typically build a floating froth nest of air bubbles in which the eggs are deposited. The bubbles may provide a supply of oxygen. Usually one or both parents stay near the nest to protect and maintain it. Froth nests have been attributed to the African characoid *Hepsetus* (which is not known to be an air-breather, but may leave its young in habitats likely to be oxygen-deficient). Nesting habits are also ascribed to characoids of the family Erythrinidae. Erythrinids tend to enter swampy regions, and *Hoplerythrinus* is evidently capable of air-breathing. *Callichthys* and *Hoplosternum*, South American air-breathing catfishes, construct froth nests, whereas the related *Corydoras*, which probably are not air-breathers, generally scatter their eggs amidst plants. In most characoids, although courtship and selection of spawning site may be highly complex, parental behavior probably ends once the eggs are deposited. There are no records of parental care in gymnotoids, excepting the unconfirmed report (Du Bois-Reymond, 1882) that *Electrophorus* (the electric eel) practices oral brooding. In *Electrophorus* a highly convoluted oral epithelium facilitates air-breathing (Carter, 1935). (There is also reason to think that *Gymnotus*, which is related to *Electrophorus*, takes the young into its mouth.) It would appear that the great majority of fishes in the Amazon and Congo have no parental care. As pointed out by McConnell (1969: 63–64) many Amazonian fishes engage in upstream spawning migrations (piracema), producing extremely large numbers of eggs per female, all or most of these eggs being laid at one time at the start of, or early in, the rainy season. In all such fishes parental care is very probably nonexistent. None of the fishes with modifications for breathing air participate in piracema.

A remarkable exception to the general rule that non-air-breathing characoids lack parental care is provided by *Copella*, the spawning and parental care of which have been the subject of several reports by aquarists (for detailed extracts from the literature and additional references see Breder and Rosen, 1966: 163–165). The main events seem clear enough. The eggs are actually deposited out of the water. A pair about to spawn station themselves at the surface beneath an overhanging object (presumably the underside of a leaf in nature) that is about three or four inches above the water. With bodies close together, the pair leap and momentarily adhere to the object. After repeated trials, the actual spawning begins. Half a dozen to a dozen eggs are deposited with each leap, until sixty or more eggs are left lying close together (but not on top of one another) in a clump of spawn resembling that of a snail. Afterwards the male returns every twenty to thirty minutes and splashes the eggs with water by making vigorous fin and body movements. Between splashings the male is stationed at a spot some distance from the eggs. The eggs hatch in two or three days, and the fry drop into the water and spend the next few days near the surface (summarized from Stoye, 1935). This fish occurs throughout much of the Amazon in backwaters and swampy places where deoxygenation is likely. This fact, as well as its small size, habit of frequently resting at the surface, and somewhat cyprinodontlike appearance suggest that it can utilize the oxygen-rich layer of water at the air-water interface. The aquarists' accounts of its spawning, parental care, and behavior of its fry are suggestive of adaptations to permit reproduction by fishes in habitats almost totally deprived of oxygen.[6]

BIOLOGICAL INTERACTIONS OF FISHES IN THE AMAZON AND CONGO

Apart from predator-prey and host-parasite relationships, with one exception there are no recorded instances of biological interactions between Amazon or Congo fishes and animals of other classes. The exception is commensalism of chironomid larvae attached to Loricariidae and Astroblepidae in the Amazon recorded by Freihofer and Neil (1967). Insects aside, invertebrates apparently are of minor consequence in the Amazon and Congo river systems. Almost all of the marine groups with which tropical reef fishes display so many complex symbiotic and commensal relationships are absent, and nothing has taken their place. The relatively scarce molluscs and crustaceans exhibit little diversity compared to those of tropical reefs. Excepting parasites, then, almost the only animals with which the fishes can interact are other fishes.[7]

Conspicuously marked Congo and Amazon fishes. Africa and South America are famous for brightly colored and strikingly patterned fishes, most of which regularly find their way into the aquarium fish trade. Such fishes are not evenly distributed among the river systems of the two continents. In general, more brightly colored fishes occur in forest rivers than in savanna rivers; and more in black water or clear water rivers than in white water rivers. The highest proportion of brightly colored fishes occurs in the river systems and in the fish groups with the highest numbers of species. The great majority of brightly colored fishes in the aquarium trade of Africa come from the Congo. The most brightly colored of all freshwater fishes are some of the small Amazonian Characidae. The trend toward more distinctively marked representatives in the Congo and Amazon basins affects almost all groups of fishes in Africa and South America. To cite just two examples from Africa: the catfish genus *Synodontis* is represented by 15 species in the Volta basin and 37 species in the Congo. None of the Volta species can match the bright colors or contrasting patterns of the Congo species *S. angelicus, S. ornatus, S. ornatipinnis, S. flavotaeniatus, S. decorus, S. nummifer*, and *S. notatus*. Again, the Volta has three species of the characoid genus *Distichodus*, all with indistinct vertical bars and drab colors, while the Congo has eleven species of *Distichodus*, all but two of them distinctively or even strikingly marked. Equally good examples could be drawn from the Characidae, the cyprinid genera *Labeo* and *Barbus*, and the anabantoid genus *Ctenopoma*. The major exceptions to the trend in Africa are the uniformly drab or cryptically colored mormyrids, in which nonvisual sensory structures are highly specialized and the eyes are reduced. In South America the gymnotoids constitute a similar exception. These bright colors and striking markings are evidently meant to advertize the presence of their possessor. The bright colors, unlike those of many gaudy tropical birds and insects, are not confined to mature males, but generally appear at an early age in all individuals. If the fishes were distasteful, venomous, or harmful in some way, we could make an hypothesis that their coloration warns away predators. At least for the majority of characoids, however (which provide most of the best examples of brilliantly colored fishes both in the Amazon and in the Congo), there is no indication whatever that they are inedible or dangerous in any way to predators. It would seem, although there are no data available to support this, that the brightly colored characins are just as subject to predation as drably colored ones, if not even more. In this respect the colors advertizing their presence are probably a disadvantage. Many of the small, brightly colored Amazonian characins form schools. This is true of the most brilliant characins of all, the neon tetras and cardinal tetras. Most of these brightly colored characins live in black water or clear water igarapés, a habitat that can be highly temporary (see p. 122). Thus populations frequently are split up or dispersed, and species recognition and schooling habits are probably important means of reconstituting populations.

Association of species of Amazonian characoids in mixed schools. Myers (1960b), Géry (1960), and McConnell (1969) recounted examples of generically distinct but similar appearing South American characoids that form mixed schools of two or more species. Myers (*ibid.*, p. 207) reported that the small characoids *Creagrudite maxillaris* and *Creagrutus phasma*, which look very similar, were collected together (it is unknown whether they were schooling together). He suggested that they appear to form an instance of Batesian mimicry, with *Creagrudite* the model and *Creagrutus* the mimic. Re-examination of fishes identified as *Creagrudite* from the same area (upper Orinoco-upper Rio Negro) revealed among them another species of *Creagrutus*, which appears to be *C. melanzonus* (Myers and Roberts, 1967). All three species have a blackish crescentic humeral blotch and are closely similar in appearance. Géry (1960) suggested that similar cheirodontines and tetragonopterines that school together both benefit from the association, and thus the mimicry is Müllerian. Géry (*ibid.*, p. 37) labelled the schools "protective associations" but did not identify the nature of the protection the association supposedly provides. As noted by McConnell (*ibid.*, p. 130) the facts are not available to show what advantages the fishes gain from such mimicry. Perhaps it permits small numbers of isolated individuals of two (or more) species to form a nucleus for aggregation with increased chances that breeding populations eventually will be reconstituted. Moynihan (1968) discussed several instances of mimicry that seem to facilitate flocking in neotropical mountain birds.

Amazon and Congo fishes of minute size. Consideration of the fishes in the Amazon and Congo that have minute body size as adults indicates that this is primarily a response to biotic pressures. In the Amazon, where biological interactions among fishes perhaps are greater than anywhere else in the world, we find more minute freshwater fishes than anywhere else, including: the smallest oviparous and the smallest viviparous cyprinodonts in the world (*Fluviphylax pygmaeus* and *Poecilia minor*); one of the smallest needlefishes (*Belonion apodion* Collette, 1966b); two tiny species of Eleotridae (*Microphilypnus* Myers, 1927); and minute catfishes in several subfamilies of Trichomycteridae, a number of them smaller than any other catfishes. Excepting the needlefish, which is very slender, every one of these is less than an inch long when fully adult. All excepting the catfishes are secondary freshwater fishes and belong to groups whose presence in the Amazon can be thought of as "marginal." Large poeciliids are absent in the Amazon except for three good-sized species of *Poecilia* that have penetrated no further inland than Pará. *Poecilia minor* itself seems confined to the Lower Amazon. It is known from only two collections (separated by more than 100 years) within 100 miles or so upstream from Obidos. *Poecilia scalpridens*, the only other poeciliid in the interior of the Amazon, and not much larger than *P. minor*, is known from a few localities in the Middle and Lower Amazon. *Fluviphylax* is a phyletically isolated form widespread in the Amazon basin. Its relationships evidently lie either with Procatopodinae, a subfamily otherwise restricted to Africa, or with Fundulinae (found mainly in North and Central America) rather than with Rivulinae (the only other subfamily of Cyprinodontidae in the Amazon basin) (Roberts, 1970a). Large gobioids occur in fresh water in many places throughout the tropics where primary freshwater fishes are poorly represented. Although a number of large gobiids and eleotrids have been recorded from the mouth of the Amazon, the two minute species of *Microphilypnus* are the only gobioids known from its interior. A third species of *Microphilypnus*, perhaps the smallest one, occurs in the Orinoco basin (Myers, 1927). The Congo eleotrid, *Kribia nana*, while considerably larger than *Microphilypnus*, is nevertheless a very small fish. It is the only gobioid in the interior of the Congo. Until recently the cyprinodont *Aplocheilichthys myersi* was the smallest fish known from the Congo basin. We may note that at least some of these little fishes (*Fluviphylax*, *Poecilia minor*, and *Kribia*) apparently reproduce all year round; probably they all do. Their size may permit them to utilize food resources unexploited by adults of other fishes. And it may place them below the size threshold for attack by most predaceous fishes.

The best African example of a fish group with an essentially marginal distribution, except for unusually small species in the midst of the richest lowland faunas, is provided by the Kneriidae. The species of *Kneria* and *Parakneria*, some of which are 80–150 millimeters long, are now known from high gradient streams around virtually the entire periphery of the Congo basin (Poll, 1966; 1969, map on p. 360) but have yet to be found in the cuvette centrale or in the main rapids of the Congo River, where one might expect ecological conditions would be suitable for them. The kneriid *Grasseichthys gabonensis* Géry (1964), only 18–20 millimeters in standard length and very slender, was discovered in 1964 by Géry in forest streams in Gabon and by myself in forest streams in the western part of the cuvette centrale. This is now the smallest known species of fish in the Congo basin.[8]

Adaptive responses to predation. McConnell (1969) noted the high number of predatory fishes in the Amazon (which she felt was relatively higher than in African fresh waters) and suggested that this permitted more prey species to co-exist. (The converse may also be true.) Of adaptations displayed by Amazon and Congo fishes that lessen the toll of predation for their possessors, reference should be made to the alarm substance and fright reaction in Ostariophysi, Kneriidae, and Phractolaemidae (Pfeiffer, 1963, 1967); the ability of gymnotoids to withstand mutilation (Ellis, 1913); the cryptic body form and coloration of such fishes as *Farlowella;* the heavy (and frequently spiny) body armor of many catfishes (especially in the families Doradidae and Loricariidae); and the protective dorsal and pectoral fin spines of most catfishes. In some catfishes these spines are very sharp and venomous, as in the Amazonian caratai, *Centromochlus heckelii*, and other auchenipterids. In other catfishes the spines are stout and can be locked in erect position. *Centrochir crocodili* (Humboldt) of the Rio Magdalena is called "mata-caiman" after the wounds it inflicts on crocodiles attempting to swallow it (Eigenmann, 1922: 47). It is said in Ghana that crocodiles sometimes are killed trying to swallow *Auchenoglanis occidentalis.* Many catfishes in the Amazon and Congo basins are equally equipped with pectoral and dorsal spines, and once they grow to a certain size they presumably are seldom preyed upon by predators that swallow their prey whole. The spines do not protect them from piranhas, which bite out chunks rather than swallow their prey whole, or from attack by various kinds of candirú (see pp. 136–138). On the other hand, the electric eel of the Amazon (*Electrophorus electricus*) and the electric catfishes of Africa (*Malapterurus*) may be entirely exempt from predation. *Malapterurus* only an inch or so long are capable of producing a jolting shock (personal observation).

Partitioning of food resources, and trophic adaptations. Another obvious aspect of biological interaction or accommodation in Congo and Amazon fishes is the partitioning of food resources. Food-place, food-time, and food-type partitioning are probably equally important. The basic dichotomy of ostariophysans into nocturnal and diurnal groups (siluroids and gymnotoids vs. characoids and cyprinoids) is mentioned in the introduction. The habitat preferences of many of the fishes in the Amazon and Congo are in many instances closely linked with feeding habits. Many of the fishes have highly modified trophic structures, some of which are quite peculiar. Interestingly enough, for some of the most peculiar types of feeding we have examples of convergence between fishes of the Amazon and Congo basins. It has been said that riverine fishes of tropical Africa and South America exhibit less trophic specialization than cichlids in lakes Victoria, Tanganyika, and Nyasa and that this is due largely to relative year-round availability of food in the lakes in contrast to marked seasonal abundance and dearth of food in the rivers. The observation and the reasoning, it seems to me, while they may be relevant in savanna rivers having extreme seasonal vicissitudes, do not apply to the Congo and Amazon rivers. In any event, it should be remembered that fishes are capable of fasting for considerable periods, provided they get an adequate share of the resources available during times of abundance. A more important reason for the relative paucity of fishes with highly specialized trophic structures in savanna rivers is probably faunal impoverishment resulting from drought. The diversity of feeding habits of fishes in the Amazon and Congo is perhaps as great as one could expect given the nature of the food available. Were it not for partitioning of food resources and concomitant evolution of specialized feeding behavior, the astounding number of fishes present in the Congo and Amazon probably would be unable to coexist. Partitioning of food resources apparently has proceeded to the point where utilization and cycling of energy and materials are very efficient. The upper limits of partitioning presumably are determined by complicated factors such as the variety of foods and their relative availability in space and time; and the capacity of fishes to exist (e. g., by fasting or facultative feeding) when such resources are unavailable, and to reproduce when they become available. Food resources cannot be partioned indefinitely, because a point would be reached where individual parcels of energy and materials are too small to support populations big enough to have sufficient probability of survival, even in habitats where catastrophic (i.e., nonbiological) causes of extinction tend to be minimal.

The main categories of food in the big tropical rivers are relatively few, namely, 1) other fishes; 2) insects, both aquatic and terrestrial, and aquatic insect larvae; 3) higher plants, including fruits and leaves fallen into the water and roots growing out into the river from the banks, as well as some aquatic plants; and 4) mud or earth, including interstitial organisms, dead organic matter, and possibly bacteria. Each of these categories seems to be highly partitioned among the fishes and to have evoked various kinds of trophic, behavioral, and morphological adaptation. It should be noted that some lake cichlids that are highly specialized for feeding on plankton and molluscs would find little or none of their predilected food in rivers of the Amazon or Congo basins.

Predatory fishes. It would appear that nowhere else on earth have fishes evolved as many manners of preying on other fishes as in the Amazon. Excluding fin-eaters and scale-eaters, in the Amazon over 40 species of characoids alone are primarily or exclusively piscivorous. The more voracious species of *Serrasalmus* (known as piranha chata in Brazil) bite out chunks from larger fishes. Géry (1963: 615–616) noted that for each species of *Serrasalmus* in the voracious subgenera *Pygocentrus* and *Taddyella* there is a geographically corresponding species in the less specialized subgenus *Serrasalmus*. He hypothesized a parallel evolution of sympatric species in which the less aggressive *Serrasalmus* (known in Brazil as pirambebas) benefited from association with *Pygocentrus* and *Taddyella*.

Several of the most archaic fishes of the Amazon and Congo basins are rapacious predators. Some species of *Polypterus* (e. g., *P. senegalus*) are insectivorous, but the two largest species—*P. endlicheri* and *P. congicus*—are piscivorous. The African osteoglossoid *Heterotis* is a filter-feeder, but the Amazonian *Osteoglossum* is piscivorous (feeding mainly on characins), as is *Arapaima gigas* (the largest osteoglossoid), which sometimes feeds on *Osteoglossum*. The African *Hepsetus*, which appears to be the most primitive characoid (Roberts, 1969), is a voracious piscivore, as are a number of phyletically isolated (and perhaps primitive) South American characoids.[9] This should not come as much of a surprise, for a remarkable number of survivors of archiac fish groups throughout the world—viz., lampreys, sharks, chimaeras, gar-fishes, bowfin, tarpon, and pikes—are extremely effective piscivores. Far from inhabiting situations geographically or ecologically isolated and open to relatively few organisms (as do survivors of some archaic invertebrate groups), these modern predaceous representatives of archaic fish groups are frequently dominant forms in shallow seas and especially in lowland rivers (e. g., the Congo) where the fish fauna is exceptionally rich.

Scale-eating and fin-eating characoids. South America has several scale-eating characoids (Roberts, 1970b). Four genera and about ten species are present in the Amazon (scale-eating has yet to be verified for all of them). Eating scales appears to be of major importance in the mode of living of these fishes. Several of the species have been observed actually feeding on scales from other fishes, and scales generally predominate in their stomach contents. Their teeth are obviously specialized for removing scales. They generally attack fishes larger than themselves, which presumably usually escape without being killed. Although the Congo is rich in characoids, no scale-eaters have been reported there. The only other freshwater scale-eating fishes are cichlids from lakes Nyasa, Tanganyika, and Victoria.

The Congo, on the other hand, has a remarkable group of fin-eating characoids, all in the family Ichthyboridae (Matthes, 1961). Most but not all members of this family will probably be implicated as fin-eaters. The small *Microstomatichthyoborus katangae* feeds on aquatic insect larvae. *Gavialocharax* (from Cameroun), with its wonderfully elongated jaws, probably is a fin-eater, as are the species of *Belonophago* (from the Congo). As with scale-eaters, they attack fishes much larger than themselves. The fin-eater diet, rich in bone minerals, probably was prerequisite for the development of the exceedingly hard, platelike dermal armor (derived from scales) present in *Belonophago* and *Phago*. Daget (1967) reported that *Ichthyborus besse besse* in the Chad basin is a fin-eater, while *Ichthyborus besse congolensis* in the Lualaba seems to have readopted secondarily the diet of a micropredator. Daget (*ibid.*, p. 142) suggested that the difference in feeding habits between the two subspecies might be explained thus: in Katanga the "ecological niche" of fin-eaters is occupied by *Phago* and *Eugnathichthys*, while *Ichthyborus*, probably less well adapted to fin-eating, has its diet restricted to small fishes and invertebrates; in the Chad basin, on the other hand, *Ichthyborus* has no competitors (no other ichthyborids occur there) and occupies only the "ecological niche" of fin-eaters. In the Amazon the only known fin-eaters are in the genus *Serrasalmus* (e. g., *S. elongatus*), and they tend to utilize other foods to a considerable degree.

Feeding habits of the Amazonian catfishes known as candirú. Candirú is an Amerindian name for certain catfishes which attack other fishes and, occasionally, man. (For a delightful account of candirú attacks on man, see Gudger, 1930.) Very little is recorded concerning their feeding habits. About 30 species have been described from the Amazon basin, representing two unrelated families of catfishes, Cetopsidae and Trichomycteridae. The trichomycterid candirús belong to four subfamilies, Pareiodontinae, Stegophilinae, Vandelliinae, and Tridentinae. During fieldwork with EPA in October and November 1968 many candirú species were collected, some of them in considerable numbers, and observations were made on their feeding behavior. Most were collected with a fine-meshed wire basket (open at one end) baited with fresh fish heads, or with a fine-meshed dipnet and a fresh fish head suspended in the water on a string. Large catfish heads worked best.

Cetopsis coecutiens (Lichtenstein) gets at least a foot long and two inches in diameter, and is the largest candirú in Amazonas. On several occasions I saw this species taken in open water in midday, on hooks baited with pieces of fresh fish. Its back is deep sky-blue, its belly milk white. It was never taken at night or by means of my fish heads. *Hemicetopsis candiru* (Spix) reaches about eight inches in length and its whole body has a pinkish or reddish hue, especially in somewhat smaller specimens. The largest specimens tend to have a more greyish cast. It is apparently active only after dark. At first none of this species were collected. Then one evening, finding myself without fresh material for bait, I tried some old fish heads from previous fishing that had been tied to the boat, and got a fair number of *Hemicetopsis candiru* and virtually no other species. (Earlier it had been noted that, in general, fish heads were most efficacious as candirú bait while very fresh.) Later on, fishing was carried out with fresh and rotten fish heads simultaneously, with the finding that *Hemicetopsis* came only to rotten baits. In this it differs from all other candirú. *Pareiodon microps* Kner reaches about eight inches long and its body is uniformly grey. It was more commonly captured than any other candirú with fish heads used as bait. On several occasions 50 to 100 were captured in a baited wire basket within an hour or two and on one occasion about 300 were caught in less than an hour. They came mainly in the first hour or two after nightfall and seemed to prefer fresh baits. *Hemicetopsis candiru* and *Pareiodon microps* feed by biting out circular chunks. If they are unsuccessful in removing a bite, they leave a nearly perfect circular scar. *Pareiodon* or *Hemicetopsis* eight inches long leave a scar about a half inch in diameter. Stomachs of these fishes frequently contain a half dozen or more round chunks of flesh or viscera. There is no evidence that either *Pareiodon* or *Hemicetopsis* enter the gill chambers or suck the blood or body fluids of other fishes.

The majority of candirú belong to trichomycterid subfamilies, Stegophilinae, Tridentinae, and Vandelliinae. These range in size from less than an inch long and extremely slender to perhaps six inches long. In Stegophilinae and Tridentinae, which are closely related, the mouth is wide, and teeth in both jaws are very numerous and arranged in several rows. In Vandelliinae the mouth is relatively narrow and the teeth are few and in only one or two rows in both jaws. According to Eigenmann (1918), Reinhardt in 1858 was the first to record that a species of candirú (*Stegophilus insidiosus* Reinhardt, from the Rio das Velhas, Rio São Francisco basin) enters the gill chambers of other fishes. Eigenmann (1918) recorded similar behavior for a species of Vandelliinae (*Branchioica bertonii* from the Rio Paraná). During the EPA fieldwork a number of Vandelliinae and Stegophilinae were obtained directly from the gill chambers of fishes caught on hook and line, usually large catfishes, and their stomachs were frequently gorged with blood. Stegophilinae and Vandelliinae were readily caught by using fresh fish head baits. *Pseudostegophilus nemurus* (Günther) were observed on only one occasion, at midday, when our boatmen were unusually successful in catching dourada and filhote (catfishes of the genus *Brachyplatystoma*) by hook and line. One specimen dropped out of the gill chamber of a dourada after it was landed and was positively identified. The *Pseudostegophilus* appeared in numbers and were darting about near the surface, even jumping clear of the water in evident excitation. Other than on this occasion, dusk and the first hour or so after nightfall appeared to be the time of greatest activity for Vandelliinae and Stegophilinae. *Pseudostegophilus,* with its handsome golden-hued body and dark cross bars, is the most colorful candirú, which further suggests that it is more diurnal than other species.

Kelley and Atz (1964) published a photograph of *Vandellia* attacking goldfish in an aquarium and reported that after gorging on blood the *Vandellia* settled to the bottom of the aquarium. Vandelliinae, except for their eyes and viscera, are generally transparent in life. *Plectrochilus* has a longitudinal black mark on the caudal peduncle and fin. Vandelliinae are slender fishes but are capable of considerable abdominal expansion to receive blood. There is no evidence that either Vandelliinae or Stegophilinae spend protracted periods in the gill chambers of another fish; perhaps members of both subfamilies gorge themselves fairly soon after entering and then swim out. Haseman (1911: 315) stated that *Vandellia* and other trichomycterids lie buried in sand bars. When disturbed the *Vandellia* "rise like a flash and bury themselves again in an instant, leaving a small round hole where they re-entered." He reported collecting four hundred *Stegophilus* buried in the sand in an igarapé near Santarém; however, his remark that these were "minute and could be seen by the millions in this locality, where the water was too shallow to permit the presence of large fishes of any kind" indicates they may have been Tridentinae instead of *Stegophilus.* McConnell (1964: 116) reported *Trichomycterus* (*Pygidium*), minute trichomycterids (Tridentinae ?), and *Hemicetopsis* amidst a large variety of other fishes (mostly catfishes) hiding in crevices and hollows in logs in a creek of the Rupununi River in British Guiana.

On one occasion I watched a fisherman return from spearing a pirarucú (*Arapaima gigas,* the largest scaled fish in Amazonas). In the bottom of his canoe were several specimens of a very dark stegophiline (identified in the field as *Ochmacanthus reinhardti*). The fisherman indicated that many such candirú had been clinging to the pirarucú as he hauled it into the canoe. Upon examining the gill chamber of the pirarucú, I could not detect any indication of damage to the tough gill filaments and strongly doubt that the *Ochmacanthus* obtained any blood from the gill filaments or elsewhere. Perhaps they were feeding on mucus, which is abundant on pirarucú. *Ochmacanthus* observed on sandy bottoms in relatively clear water were always light colored. I suspect they can change color to match the substrate, whether it be light sandy bottom or the dark body of a pirarucú.

Mr. Jonathan Baskin, who is studying the family Trichomycteridae, called to my attention the scale-eating habit of the stegophiline *Apomatoceros alleni* Eigenmann. The mouth of this species is capable of being everted to form a discoid sucker about twice as wide as the head, and is provided with numerous bands of teeth. The evidence of scale-eating is provided by examination of an alizarin preparation and radiographs of two specimens (105 and 111 mm, catalogued as no. 109804 in the fish collection of the Academy of Natural Sciences of Philadelphia), the alimentary canals of which are partially filled with scales about 3 millimeters long.

The food habits of the Tridentinae are unknown. All are small (usually an inch or less in length). We collected several species of this subfamily by using rotenone in shallow, forested backwaters wth deeply tinted, clear water at localities along the Rio Solimões between the Rio Purus and Rio Içá, but no observations were made on their behavior.

Amazonian fishes with trophic structures for straining minute organisms from midwater. Production of phytoplankton is practically lacking in most Amazonian waters and zooplankton is often absent. In black waters and white waters this is probably due mainly to the low penetration of light. The big black water rivers with wide mouth-bays have very little primary production of phytoplankton, partly because the water is highly acid and extremely poor in inorganic ions and nutrients. An insignificant amount of phytoplankton, mainly of desmids, and more surprisingly, a certain amount of zooplankton may be present. The principal biotopes in which phytoplankton develops are the mouth-bays of clear water affluents, such as the Tapajós and the Xingú, and the shore lagoons or lagos of white water rivers. In some places veritable plankton blooms occur. The shore lagoons are often favored fishing grounds. Fishes are scarce in the mouth-bays, however, and the main consumption of the phytoplankton produced in them may happen in the white water rivers into which they flow (Sioli, 1968).

A number of Amazonian fishes have trophic structures that could permit them to utilize plankton. Böhlke (1953) described a minute (25–30 mm) herringlike characid from the upper Rio Negro, *Thrissobrycon pectinifer,* with "otter-board" maxillaries in a nearly toothless mouth and about 25 long gill rakers on the lower limb of the first gill arch. Böhlke inferred that it is an open-water, schooling planktophage. Amazonian clupeids and engraulids tend to be predators, but *Cetengraulis jurnensis* Boulenger, with about 40 long, finely denticulate gill rakers on the lower limb of the first gill arch, is probably planktophagous. The Amazonian fishes with the most highly modified apparatus for straining minute organisms from the water are the catfishes of the genus *Hypophthalmus* and the characin *Anodus elongatus* and one or two of its close relatives. In these presumably planktophagous catfishes and characins the mouth is toothless and the gill slits are extremely long. The gill membranes are free from the isthmus. The gill openings and gill arches extend anteroventrally almost to the symphysis of the lower jaw, so that virtually the entire floor of the oropharyngeal cavity is lined with gill rakers. The gill rakers on all of the gill arches are elongate and exceedingly numerous. There are no less than three very distinct species of *Hypophthalmus* in the Amazon. At least one of them gets to be two feet long. In Brazil they are called mapará. The ventrally directed eyes and laterally compressed body with its complicated system of criss-crossing lateral line canals make the genus readily recognizable. The trophic structures are highly distinctive. The opening of the mouth is large and its roof is smooth. Most of the gill rakers are borne on the elongate lower limbs of the gill arches. A 300-millimeter specimen of *H. edentatus* has about 240 gill rakers are borne on the elongate lower of the gill rakers tapers off at either end of the gill arch, but most of them are extremely long, about 15–17 millimeters. Rakers on succeeding arches are almost as numerous as those on preceding arches, and only slightly shorter. The first two arches bear rakers on the leading edge only; the full length of the trailing edge of these arches supports a strong membranous flap the height of which is about one-half of the length of the gill rakers. The third and fourth arches bear rakers on both leading and trailing edges, and no flap. The fifth arch bears rakers on its leading (free) edge. The mouth, branchial arches, and gill covers can be held in such a position that all water leaving the gills must first pass through a fine sieve formed by the rakers (observed by manipulation of preserved specimens). The tips of the gill rakers of the trailing and leading edges of the third, fourth, and fifth gill arches meet to form a ΛΛΛΛΛ-shaped sieving mechanism. For this to be completely effective all the water must exit through the third and fourth gill slits. The membranous flaps on the trailing edges of the first and second gill arches presumably prevent water from exiting through the first and second gill slits. *Hypophthalmus* form large schools and undergo extensive migrations. They are one of the most important food fishes in the lower Tocantins and are among the fifteen or so commonest species in the fish market at Manaus.

The highly streamlined *Anodus elongatus* appears to have an even more perfect straining mechanism than *Hypophthalmus*. Both leading and trailing edges of its first four gill arches bear rakers, and the fifth arch bears rakers on its leading (free) edge. The upper limbs of the arches are about two-thirds as long as the lower limbs and bear correspondingly fewer rakers. The number of rakers is only slightly reduced on successive arches. The first arch of a 200-millimeter specimen bears 80 + 110 rakers, most of which are 10 or 11 millimeters long. The dorsal edge of each raker bears two rows of about 100 or more tiny denticles approximately 0.2–0.3 millimeters long and 0.1 millimeter apart. The denticles of adjacent rakers mesh to form an exceedingly fine sieve. The stomach is thin walled and the intestine relatively straight. In the specimens examined by me, collected by the Thayer Expedition, the stomachs are empty. A related form, *Eigenmannina melanopogon*, from the upper Amazon has exceedingly numerous gill rakers, and is also presumably planktophagous.[10]

In the Congo basin none of the catfishes or larger characins are planktophagous. The small characin *Clupeopetersius schoutedeni* Pellegrin in Lake Tumba is a pelagic planktophage (Matthes, 1964: 43, figs. b and d, pl. 1), as are some endemic Congo species of Pellonulinae.

Parallelism in the feeding habits of mormyroids and gymnotoids. The nature of the electric faculties and their biological significance in gymnotoid and mormyroid fishes is now under intensive investigation; evidently a great deal remains to be discovered and understood (the best general review is still Lissmann, 1958). This independent evolution of weakly electrogenic freshwater fishes in Africa and South America is a particularly striking example of parallelism because of its novelty and the pervasiveness of its effects. Some 18 genera and 35 species of gymnotoids have been recorded from the Amazon basin. Undescribed Amazonian species are present in most important museum collections and the group is in great need of systematic revision. Ten genera and 93 species of mormyroids have been recorded from the Congo basin. It is believed that all mormyroids and gymnotoids possess both electrogenic and electrosensory faculties, and this has been verified for at least one species in almost every one of the genera. In both groups it is apparent that virtually all aspects of the morphology and behavior have become specialized and integrated with the electric faculties. Certain aspects remain uninvestigated. For instance, it is known that electrosignalling functions in territorial and aggressive behavior in gymnotoids and mormyroids, but its (presumably important) role in sexual behavior has not been described in either group.

The parallels in habitat selection, mode of locomotion, and feeding habits between gymnotoids and mormyroids are intimately bound up with their electric faculties, although this has not been fully appreciated and much remains to be learned concerning it. It is my belief that elucidation of the interrelations between electric behavior and feeding habits in mormyroids and gymnotoids will contribute materially to understanding the evolutionary history and perhaps the very origin of both groups. The strongest evidence that electric behavior has profoundly affected feeding habits in mormyroids and gymnotoids lies in the repeated development in both groups of highly peculiar and remarkably similar trophic structures, e. g., diverse types of elongated tubular mouths with weak jaws and feeble dentition. These structures evidently permit efficient exploitation of a rich bottom fauna of small worms and wormlike insect larvae (e. g., enchytraeids and chironomid larvae) which other fishes can use only marginally or not at all. (For food habits of gymnotoids, see Ellis, 1913. Little comprehensive information is available on mormyroid food habits. For food habits of Congo mormyroids, see Matthes, 1964. Observations of mine and a few published accounts confirm that some mormyroid species feed heavily on chironomid larvae.) It seems likely that several factors enter into this relationship between electric faculties and feeding habits. The nocturnal behavior of some gymnotoids and mormyroids may mean that they are feeding actively when such wormlike prey is most susceptible to predation. But this in itself seems insufficient to account for the successful exploitation evidenced. Two further possibilities merit consideration. The first is that mormyroids and gymnotoids are able to locate such minute prey electrosensorily. I think this highly likely. The second is that the weak electric emanations of gymnotoids and mormyroids affect these prey in a manner that makes them more susceptible to predation. Either of these last two possibilities (or both acting together) would, in my opinion, go a long way towards explaining the evolution of almost all of the more peculiar trophic modifications exhibited by mormyroids and gymnotoids. I would go even further, and suggest that the interrelation between electrical faculties and feeding played a decisive role in the initial divergence of the gymnotoids and mormyroids from nonelectrically specialized ancestors.

Bottom feeding fishes with generalized trophic structures. Roughly a third of Amazonian and Congo fishes are bottom feeders. Mormyroids and gymnotoids, and Chilodontidae and Hemiodontidae among the characoids, are highly selective in removing food items from substrate. Most bottom feeders, however, including members of the large South American characoid family Curimatidae, cyprinids of the genus *Labeo,* and many catfishes, ingest considerable amounts of substrate with their food. No serious efforts have been made to determine what part of the ingested material these fishes digest. Obviously this will be difficult to work out. The food may be in virtually unrecognizable condition before ingestion, and is liable to be taken in with all sorts of nonnutritional material. Nevertheless, partitioning of food resources probably occurs in these bottom feeders. At first glance, the manner of ingesting quantities of bottom material might seem to preclude fine selection of food resources, but I expect this contention would disappear if we had more information about habitat selection and substrate preference of the bottom feeders.

One of the main reasons African characoids are less diverse than those in South America appears to be that in Africa other fish groups pre-empted certain major food resources. Mormyroids and cyprinoids, to cite what appear to be the two most important examples, appear to have largely or entirely taken over bottom feeding niches that might otherwise have been available to characoids. None of the African characoids, with the possible exception of *Citharinus,* have bottom feeding habits comparable to the Prochilodontidae and toothless Curimatidae of South America. In the Congo the cyprinoid genus *Labeo,* which parallels the family Prochilodontidae in certain respects, is represented by at least 22 species, most of them endemic. Much of the present diversity of African and South American characoids is probably due to relatively late radiations, and in Africa these radiations occurred in competition for food resources with a greater number of other fish groups.

Trophic specialization evidently played a major role in the adaptive radiation of characoids. The variety of characoid teeth, from simple conical elements to highly unusual forms of multicuspid teeth, is unparalleled by any other living group of vertebrates except mammals. The peculiar modes of tooth formation and tooth replacement characteristic of characoids apparently arose early in their history and provided the main morphological variations that led to the evolution of diverse feeding habits. These have been described and discussed elsewhere (Roberts, 1967).

Feeding habits of fishes in small Amazonian rain-forest streams. The stomach contents of 49 fish species from three rain-forest streams near Manaus were reported on by Knöppel (1970). His main conclusions (pp. 343–346) were:

1. Terrestrial insects (especially ants), aquatic insect larvae (especially Ephemeroptera and Trichoptera), and vegetable remains are major items in the stomach contents.
2. Most species exhibit considerable variability in the items ingested, and stomach contents of various families are relatively uniform.
3. Stomach contents of the same species collected at different times of the year (May, July, and November) are generally similar.
4. The fishes find their food in the whole living space, even those species that appear to be adapted to certain zones in the stream.
5. Distinct specialists in food ingestion are not present in the forest streams studied.
6. Neither the structure of the snout and denture, nor the morphological structure of the alimentary canal, nor even the intestinal ratio can be used as indices to the feeding habits.

The last three conclusions are too sweeping even as broad generalizations, and are not entirely in accord with statements in the main body of Knöppel's paper. Thus *Helogenes* and *Pyrrhulina* "picked up food nearly exclusively at the surface . . . yet most fishes find their food at the bottom" (*ibid.*, p. 341). The stomach contents of *Hoplias, Bryconops, Poecilobrycon, Iguanodectes, Pyrrhulina, Steatogenys, Eigenmannia, Curimatus, Chilodus, Cichla,* and many other forms reported on by Knöppel are precisely what one would expect from the morphology of their trophic structures. The numerous, sharp conical teeth of *Hoplias* are clearly those of a piscivore, and Knöppel found that adult *Hoplias* ingested only fishes (*ibid.*, p. 272). The fan-shaped teeth of *Poecilobrycon* and *Iguanodectes*, with numerous small cusps, are adapted to feeding on filamentous algae, and Knöppel found that considerable amounts of filamentous algae were ingested by *Iguanodectes* and *Poecilobrycon*. Dentition of similar appearance occurs in many small characids, and it is predictable that filamentous algae is an important food item for at least some of them. Concerning intestinal ratios, adult Curimatidae have extremely convoluted intestines, and this corresponds with their habit of ingesting large amounts of fine detritus, only a small (?) portion of which is nutritional. In six specimens of *Curimatus spilurus*? from 26.0 to 42.3 millimeters in standard length Knöppel found "sand (40%) and detritus (54%) in all stomachs"; in one stomach there was plant matter (*ibid.*, p. 276). While juvenile *C. spilurus* have "only a few concentric coils on the stomach sac" (*ibid.*, p. 335), I find that a 100-millimeter specimen has 21 concentric intestinal coils, some partly folded over on themselves, the entire mass filled with mud and occupying a space considerably greater than the space occupied by the stomach. The intestines are also extremely convoluted in *Curimatus latior*. Knöppel found that the stomach of a 151-millimeter specimen of this species contained "gray-black, very fine sand, and some larger grains" (*ibid.*, p. 276). One can also learn to recognize the morphology of trophic structures indicative of a mixed diet. Characid omnivores, for example, usually have moderate numbers of tri- to quinqui-cuspid teeth.[11]

The generalization about the relative lack of narrow trophic specialists in such small Amazonian streams is partly valid. Most of the highly specialized predatory characoids, such as piranhas and scale-eaters, are entirely absent. The commonest piscivore is probably *Hoplias*, which swallows its prey whole. Many nonpredaceous characoids with highly specialized trophic structures do not occur in small streams. Hemiodontidae, Prochilodontidae, and most genera of Anostomidae are absent. On the other hand, few fishes are more "distinct specialists in food ingestion" than the leaf fish *Monocirrhus polyacanthus*, one of the species studied by Knöppel, which feeds exclusively on small live fish (see Liem, 1970). Rhamphichthyid gymnotoids also have specialized means of ingesting their small prey.

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NOTES

1. Poll (1964) described *Congothrissa* from the cuvette centrale and designated for it a new family, Congothrissidae. Its relationships are discussed by Poll et al., (1965) and Thys van den Audenaerde (1969). It probably should be referred to the Pellonulinae.

2. The record of *Arius africanus* Günther from Stanleyville (Nichols and Griscom, 1917: 716) is probably a mistake. The specimen upon which it is based should be in the American Museum of Natural History. A recent search for it there was unsuccessful and it is presumed lost.

3. Specimens of sharks and sawfishes from the Amazon River have yet to be examined by persons competent to identify them. The Amazonian shark presumably is *Carcharhinus leucas*, the same species that occurs in Lake Nicaragua. A shark that probably was this species was photographed at Iquitos (Myers, 1952). Both *Pristis pectinatus* and *P. perrotteti* might be expected, at least in the lower Amazon. The Museum of Comparative Zoology possesses a watercolor by J. Burkhardt of a specimen of *Pristis perrotteti* taken by the Thayer Expedition at Pará on August 14, 1865, with the pencilled comments "Je possède un morceau du bec de ce poisson de Monte Alegre" and "M. le Col. Michille m'a dit qu'on en avait pris de'le Rio Madeira, au-dessus de Borba."

4. *Gnathodolus bidens* Myers (1927), a remarkable anostomid, is known only from the type specimens collected at the Orinoco-Casiquiare bifurcation.

5. Poll (1959: 160–161) considered the possibility of endemic fish species in Stanley Pool and concluded that there probably are none. Of 13 species he listed that were known only from Stanley Pool, five were subsequently recorded from Yangambi (Poll and Gosse, 1963).

6. The fish aquarists have observed depositing its eggs out of water is definitely not *Copeina arnoldi* Regan, but is probably either *Copella nattereri* Steindachner or *Copella compta* Myers (personal communication from G. S. Myers). Neal Foster has called my attention to the account of "*Copeina arnoldi*" spawning on a leaf above the water in their aquarium by Nieuwenhuizen (1964: 156–159), which is illustrated by excellent photographs. The fish in the photographs are *Copella*.

7. Most of the main rivers and streams in the Amazonian lowland are relatively poor in numbers of kinds and of individuals of molluscs and crustaceans. This is also true of the Congo. The paucity of these two groups is particularly striking when compared to their richness and abundance in lowland streams of portions of Southeast Asia. Aquatic leeches also seem to be more abundant in Southeast Asia. Perhaps molluscs, crustaceans, and leeches would be less abundant in Southeast

Asia if the dominant ostariophysans there were characoids instead of cyprinoids. G. R. Smith informs me that shrimp are fairly abundant in some Amazonian headwaters. This may be related to the relative paucity of their fish fauna. Many molluscs and crustaceans presumably would find black water habitats acidic and too poor in calcium and white water habitats too silty.

8. *Grasseichthys* is not the only minute kneriid in Africa. *Cromeria nilotica*, which attains a maximum standard length of about 28 millimeters, occurs in the main courses of the White Nile, Upper Niger, Mayo-Kebbi, and Volta rivers. It evidently spends much of its time buried in the sand. Because of its larval appearance, it was suggested at one time that *Cromeria* might be the young of an undescribed species, but no other kneriids have ever been reported from any of the basins in which it lives.

9. The characoid *Agoniates* is remarkable in feeding on other fishes when it is very small. On October 15, 1968, five specimens about 1–1½ inches long were caught in the Rio Solimões above Florianopolis. The stomach of each one was bulging with two or three cichlid young 5–8 mm long. Young *Agoniates* have rapacious dentition similar to that of adults. At this size most predaceous characoids (e. g., *Hydrocynus*) are probably insectivorous. *Agoniates* grows to about 150 mm.

10. *Anodus* and *Eigenmannina*, constituting the subfamily Anodontinae, are placed in the family Curinatidae by Eigenmann and Eigenmann (1889), Regan (1911), and Greenwood et al., (1966). This relationship, if true, is of considerable interest because in other Curimatidae gill rakers are absent or greatly reduced. All or almost all of the species are deposit feeders with highly convoluted intestines. Observations of mine indicate that *Anodus* is closely related to *Hemiodus*. The relationships of the families Hemiodontidae, Curimatidae, and Prochilodontidae to each other and to other characoid families are worth study.

11. Most of the small- to medium-sized Amazonian Tetragonopterinae (roughly 140 species) probably feed on whatever comes in their way (McConnell, 1969), benefiting greatly from insects falling into the water or emerging from aquatic larvae. The medium- to small-sized African characids allied to *Alestes* (about 40 species in the Congo) probably have similar feeding habits. In a remarkable instance of parallelism, the complex dentition of many small species of South American Tetragonopterinae (comprising a high proportion of species in the five largest genera of Characidae) is practically identical to that in small species of African Alestiinae. In these small characids of both continents, there are typically two rows of teeth in the upper jaw and two rows in the lower jaw; in the upper jaw the outer row consists of four to six relatively small and widely spaced tricuspid teeth, the inner row of eight to 16 multicuspid teeth; in the lower jaw the outer row consists of eight to 16 multicuspid teeth, the inner row of two relatively small conical teeth near the symphysis of the jaws. Occlusion apparently occurs only between the inner row of teeth in the upper jaw and the outer row in the lower jaw. Usually the number of cusps in these teeth is from three to five, but there are forms with as many as 20 cusps on each tooth. Some of the South American forms have conical teeth on the maxillary but these are usually small and apparently with little or no functional significance; the African forms invariably lack maxillary teeth. Poll (1967b) figured the dentition in most of the Congo species. In very general terms, the species with few cusps probably tend towards insectivory; those with intermediate numbers of cusps to mixed insectivory-herbivory; and those with the most cusps to herbivory.

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